Long distance Transport of Spores of *Puccinia graminis tritici* in the southern Hemisphere

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WATSON, I. A., and DE SOUSA, C. N. A. Long distance transport of spores of *Puccinia graminis tritici* in the southern hemsiphere. *Proc. Linn. Soc. N.S.W.* 106 (4), (1982) 1983: 311-321.

Evidence is presented that viable uredospores of the wheat stem rust fungus *Puccinia graminis tritici* reached Australia from Africa in 1968-69. Two strains 326-1,2,3,5,6 and 194-1,2,3,5,6 both very dissimilar from any previously found in Australia were collected in 1969 from Clinton, S. Australia and Tichborne, N.S.W. respectively. These strains or derivatives from them were found to be indistinguishable from their African counterparts. The weather systems responsible for the transport of the spores across the Indian Ocean are discussed.

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INTRODUCTION

Rust pathogens of cereals are widely distributed throughout the world and survive on native or introduced host plants. Regardless of the geographical area, these pathogens exist as a multiplicity of strains differentiated by their pathogenicity, morphology, physiological and other characters. The origin of this variability can be attributed to a number of different causes. Both sexual and asexual processes may proceed side by side in some countries but where the alternate host is insignificant, mutation can explain most of the variation.

It is generally recognized that where geographical areas are isolated the rust flora of those areas becomes characteristic of them. The extent of the differences between areas will depend on the amount of recombination occurring within them due probably to sexual reproduction in the fungus and on the survival of mutations. One of the most outstanding examples of this geographical isolation is seen in the linseed rust fungus *Melampsora lini* (Pers.) Lév. When comparisons are made between isolates from North America and Australia, Bison is found to be susceptible in the former but highly resistant to a group of strains in Australia. Strains avirulent on Bison in Australia commonly survive on the native flax *Linum marginale* Cunn. which has not yet been shown to have specific genes for resistance.

It has already been pointed out (Watson, 1977) that on a global basis the total variation in *Puccinia graminis* f.sp. *tritici* Eriks. and Henn. that can be demonstrated in any one area is related not only to sexual reproduction and mutation but to the extent of wheat breeding activities especially where programs have made use of gene specific resistance. Reports appearing in the literature however do not always give the true picture of the range of variability, since the latter is revealed only when suitable single gene differentials are used in the survey work. In *Puccinia graminis tritici* maximum variability occurs in North America where the alternate host is common and a large effort is expended on breeding resistant cultivars using the well documented *Sr* genes. There is thus extensive variation around the genes of the standard set of differentials and also around the *Sr* genes of the parents used by the breeders.

In Australia by contrast, there are few standard races, but a multiplicity of components have evolved within each following mutation and the cultivation of resistant wheats of diverse genotypes. Once these variants of the population have been

catalogued and described any spectacular deviations from them can be easily recognized and will indicate that something other than normal evolution has occurred.

TRANSPORTATION OF SPORES

(i) *Over Land areas*. Pathogen gene flow between regions will tend to have a unifying effect on their rust flora. The effectiveness of wind transport of spores in contributing to this uniformity will depend on the proximity of the regions and any impediments offered by natural barriers. It is suggested that eastern and western Europe may be different regions (Hogg *et al.*, 1969) but the rapid spread of race 77 of *P. recondita* Rob. ex Desm. following the release of wheats with the IB/IR translocation indicate that there is a ready exchange of spore material over most of this land area. The distances covered by any one spore movement are probably relatively short and seldom exceed 500–700 km (M. Boskovic, personal communication).

It has been known for a long time that spores of *P. graminis tritici* are transported on the North American continent along the *Puccinia* pathway, but the extent of the distances covered in any one step is not clear from the reports. As in Europe it would appear to be of the order of several hundred km (Hogg *et al.*, 1969).

On the Australian continent the movement of spores of *P. graminis tritici* over much longer distances and in different directions has been well documented over the last 25 years (Hogg *et al.*, 1969). The results from earlier work were confirmed in 1973. In that year practically no stem rust was found in Western Australia but there was an epidemic in the eastern states. The composition of the flora in both the east and west was well known. Sometime after this epidemic 12 strains of eastern origin were isolated in Western Australia for the first time (Luig, 1977). Presumably the spores were caught in the anticyclones which may extend for 6,000 km and which, in the November-April period, feature easterly winds over the continent. Spores must have been transported about 3,500 km from east to west over the harsh inland because there are no congenial hosts between the areas which were the source of the spores and the points of new infections.

(ii) *Over Seas*. Adjoining countries seldom present any barriers to the movement of rust spores but as they become increasingly separated by seas such as the Mediterranean, the Baltic and the Tasman, the possibility of spore transport from one to the other is reduced. From the summary presented by Hogg *et al.* (1969) it is clear that movement of rusts across water is readily occurring in Europe and spores in transit have been trapped in the atmosphere. While there is no reason to doubt this movement of *P. graminis tritici* the designation of the strains involved has not been very precise as only the broad categories of standard race numbers were known.

Hirst and Hurst (1967) believe that to establish proof of aerial dissemination of spores there needs to be 'incontrovertible association between the source and new colonies' or 'interception of migrant spores'. Work in the Australia–New Zealand area has adhered rigidly to the first of these requirements and where spore movement of rusts is postulated, the extensive genetic markers in the material at the source and at the new site have been identical as far as is known.

There are several reasons why, despite the extent of the land and water in this geographical area, the rust organisms can be so accurately characterized. First, the annual race survey has been in progress for 60 years and for much of that time the classification of the strains has been very precise because the genes involved in differentiation have included those of the standard series as well as those in the Australian supplementals. Consequently it has been possible to relate to some extent the local flora with that found overseas. Second, and very important, Australia is an isolated con-

tinent, politically uniform so that collections from a vast area can be made and examined at will. Since wind currents transport spores around the country the national wheat crop in years of favourable climatic conditions must serve as a huge biological trap to snare not only local inoculum but an occasional viable spore that may reach the continent from elsewhere. Because of this isolation it has been possible to construct an evolutionary pathway for the rusts of the Australia-New Zealand area in which the important events have been underlined (Watson, 1981; Burdon *et al.*, 1982).

A third factor in the build-up of knowledge on rust epidemiology is the continuous documentation of the population structure of the New Zealand rusts. Arrival of a new rust in Australia is followed after a short interval of some months by its isolation in New Zealand (Hogg *et al.*, 1969; Luig, 1977). There is now irrefutable evidence that cereal rust spores are transported across the Tasman Sea at frequent intervals, a distance of at least 2,000 km.

(iii) *Over Oceans*. There are as yet no reports of wind-borne inoculum of *P. graminis tritici* having crossed any of the world's oceans. With the discovery of the coffee rust organism (*Hemileia vastatrix* Berk. & Br.) in Brazil in 1970 it was suggested (Bowden *et al.*, 1971) that since trade winds blow frequently and for long periods across the Atlantic Ocean spores of this organism had been transported from the African continent. Since the strains observed on the two continents showed similar characters this appeared likely but Ingold (1978) believes there is some doubt as to whether this organism is normally dispersed by wind.

Australian workers have speculated on the possible overseas origin of several strains of *P. graminis tritici* that have successfully colonized this country. Luig (1977) discusses this in some detail but gives no data to pin point the origin of any strain common to the area. The original six standard races found 60 years ago were characteristic of Australia but no origin for them has been suggested. Luig (1977) described how these and other rusts were replaced with the passage of time by more aggressive strains. Three periods 1925, 1948-54 and 1968-69 are important in this replacement.

Entry of new rusts to the country at those times probably involved wind transport of spores across the great distances of the Pacific or Indian Oceans. The possibility of accidental or deliberate introduction by man must be largely discounted since communication between the critical areas of Australia and Africa would be minimal.

In the period 1948-54 standard race 21 was isolated as a type completely new to Australia. This race was at the time among the most common in the world but there were no comparative data from overseas to suggest from where it came. Almost 20 years later in 1968-69 further dramatic changes occurred in the population of *P. graminis tritici* in Australia. Intensive investigations were commenced to uncover the possible origin of the strains involved in this latest event.

Isolation of Strains from Africa and a Comparison with their Australian Counterparts

(i) *Early suggestions of Similarities*. Luig (1977) has already outlined some of the details concerning studies of two Australian strains of *P. graminis tritici* which differed markedly from any previously isolated in this area. Both collections had been made in 1969 by the senior author, one 326-1,2,3,5,6 from Clinton, S. Australia, the other 194-1,2,3,5,6 from Tichborne, N.S.W. The material on which each was collected had few large isolated pustules and carried the gene *Sr*6.

Although these collections were part of the annual race survey conducted by Luig and Watson the identifications revealed something unique. The first clue that overseas

inoculum may have been involved in the origin of these two rusts came from data sent by Dr J. C. Santiago who was then at Elvas, Portugal. These data showed that standard races 194 and 222 were present in Mozambique and there was evidence that pathogenicity on some lines of the Australian supplementals was the same as that of the two new local rusts. In order to make detailed comparisons of rusts from the two continents inoculum was requested from Angola, Rhodesia (now Zimbabwe) and Mozambique.

(ii) *Detailed studies of Pathogenicity of African rusts.* Two collections were received from Angola, one from Nova Lisboa the other from Caconda. A single collection was sent from Salisbury, Rhodesia. Because these collections were from overseas, strict quarantine precautions were taken during the studies with them. All tests were made in glasshouses at the University of Sydney, Glebe, thus minimizing the possibility of spores escaping and lodging on a congenial host. At the conclusion of each test the plant material and the rust were collected and destroyed.

The strain components of the three collections were identified using the differentials of Stakman *et al.* (1962), supplemented by the eleven local differentials adopted in Australia by Luig and Watson (1977). After the initial multiplication of spores, inoculum was placed onto certain key varieties *viz*. Marquis (*Sr*7b), Reliance (*Sr*5), Acme (*Sr*9g), Einkorn (*Sr*21), Vernal Emmer (*Sr*9e), McMurachy (*Sr*6), Yalta (*Sr*11) and C.1.12632 ($SrTt_1$). Many isolations were made and finally from single pustules five strains were identified from Nova Lisboa and one from Caconda. Two strains were found in the Salisbury material. According to the classification of Luig and Watson these were designated as in Table 1 and the seedling infection types on certain wheats are given in Table 2.

The two Rhodesian strains were differentiated on Acme and Barleta Benvenuto and no differences could be found between Rhodesia 2 and Angola 4. Although all differentials were tested, complete separation of the strains was possible using only those five of Table 2.

(iii) *Studies on the Australian counterparts.* As indicated above large isolated pustules were found in 1969 at Clinton, S.A. Laboratory tests showed this culture 69822 to be of strain 326-1,2,3,5,6. As reported by Luig (1977) this combination 1(*Sr*6), 2(*Sr*11), 3(*Sr*9b), 5(*Sr*17), 6(*Sr*8) of virulences had not been previously reported in Australia. Moreover and very spectacularly, this strain was avirulent on plants with *Sr*7b a host-parasite interaction that had not been seen in Australia for about 30 years. The strain was clearly new to the population.

TABLE 1

Strains of P. graminis tritici *isolated from Angola and Rhodesia*

Culture Number		Location	Australian Designation
Angola	1	Nova Lisboa	194 — 1,2,3,5,6,7
''	2	''	194 — 1,2,3,5,6
''	3	''	343 — 1,2,3,5,6
''	4	''	222 — 1,2,3,5,6,11
''	5	''	194 — 1,2,3,5,6,*
''	6	Caconda	222 — 1,2,3,5,6
Rhodesia	1	Salisbury	34 — 1,2,3,5,6
''	2	''	222 — 1,2,3,5,6,11**

* Acme mesothetic
** As Angola 4

TABLE 2

Seedling infection types on key differentials selected from the standard and local sets when inoculated with seven strains of P. graminis tritici *from Angola and Rhodesia*

Differential		Rust Cultures from						
Standard	Local	Angola						Rhodesia
		1	2	3	4	5	6	1
Marquis *Sr*7b		4	4	2	4	4	4	4
Reliance *Sr*5		0	0	4	4	0	4	4
Acme *Sr*9g		;2 =	;2 =	;2 =	;2 =	X	;2 =	4
	Norka *Sr*15	4	X	X	X	X	X	X
	Barleta Benvenuto *Sr*BB	X	X	X	4	X	X	X

Shortly after the collection at Clinton was made culture 691042 was found about 1,000 km east at Tichborne, N.S.W. It was classified as 194-1,2,3,5,6. Hence within a short time two rusts vastly different from any previously seen in this country were recovered. They differed only in the infection types found on plants with *Sr*7b. Luig however, in unpublished work, has shown that although avirulence on plants with *Sr*15 had been found before in Australia these two strains produced a distinctly lower infection type on plants with *Sr*15 than all other Australian strains with *P*15.

At the time of commencement of these studies in 1972 we had access to both these strains, but on comparing the African rusts it was found that only one, Angola 2 (194-1,2,3,5,6), had an Australian counterpart even though six of them had the numbers 1,2,3,5,6. Both 326 and 194 are avirulent on plants with *Sr*5 and a careful search was made for variants of them with virulence. Strain 326-1,2,3,5,6 was soon predominant in southern Australia and since Summit (*Sr*5) was widely grown in Victoria the appropriate mutation could be anticipated. This did not appear, however, until the rust epidemic of 1973 when at Kerang, Victoria, one of us (I.A.W.) collected rust (culture 73879) on a roadside plant of *Hordeum leporinum* Link. It was identified as 343-1,2,3,5,6 and represented the second counterpart of the African rusts, in this case Angola 3. The third counterpart was of Angola 6 (222-1,2,3,5,6) and this was collected at Willowie, S. Australia in 1974 (culture 74220). Luig and Watson later identified a fourth counterpart (culture 74654) 194-1,2,3,5,6,7 (Angola 1) at Yacup in W. Australia in 1974-75 and it was used in some of the tests.

(iv) *Comparison of the Pathogenicity of the Angola strains and their Australian counterparts.*

(a) On the standard and local differentials. When the components of the African collections had been purified and when from the survey of Luig and Watson it was found that in the Australian wheatfields counterparts of at least three of them were present, detailed comparisons were commenced. The Angola numbers were 2(194-1,2,3,5,6), 3(343-1,2,3,5,6) and 6(222-1,2,3,5,6). The corresponding three Australian cultures were 691042, 73879 and 74220.

The six cultures were used in pairs to inoculate seedlings of the standard and supplemental differentials. The infection types of the Angola cultures are presented in Table 3 and were identical with those of their respective counterparts. From these readings it was apparent that the only genes important in the differentiation of the six cultures were *Sr*5 and *Sr*7b. We concluded that this set of genetic material could not be used to distinguish between the members of each pair of strains.

(b) On entries in the International Virulence Gene Survey. At the time of analysing the African collections one of us (I.A.W.) was involved in testing the pathogenicity of

TABLE 3

Seedling infection types at 17–22 °C of 11 standard differentials and 11 local supplementals when tested with the three strains of P. graminis tritici *from Angola*

Standard Differential	Angola Culture and Strain			Australian Supplemental	Angola Culture and Strain		
	2 194-1,2, 3,5,6	3 343-1,2, 3,5,6	6 222-1,2, 3,5,6		2 194-1,2, 3,5,6	3 343-1,2, 3,5,6	6 222-1,2, 3,5,6
Little Club	4	4	4	1 McMurachy *Sr*6	4	4	4
Marquis *Sr*7b	4	2	4	2 Yalta *Sr*11	4	4	4
Reliance *Sr*5	0	4	4	3 W2402 *Sr*7b *Sr*9b	4	2	4
Kota	4	4	4	4 C.I. 12632 *Sr*Tt_1	;1 =	;1 =	;1 =
Arnautka	4	4	4	5 Renown *Sr*7b *Sr*17	4	2	4
Mindum	4	4	4	6 Mentana *Sr*8	4	4	4
Spelmar	4	4	4	7 Norka *Sr*15	X	X	X
Kubanka	;2 =	;2 =	;2 =	8 Festiquay *Sr*30	;2	;2	;2
Acme *Sr*9g	;2 =	;2 =	;2 =	9 *Agropyron intermedium*	;	;	;
Einkorn	;1-	;1-	;1-	10 Entrelargo de Montijo	2 ±	2 ±	2 ±
Vernal	;1-	;1-	;1-	11 Barleta Benvenuto *Sr*BB	X	X	X

several Australian strains on seedlings of a collection of 117 wheats. These had been selected as part of a survey to catalogue on a world basis the geographic location of virulence genes and combination of them. The group had been divided into six sections according to the alleles they carried.

Group 1 Alleles with world wide usefulness as differentials. *Sr* genes such as 5,6,8,9b,11 and Tt_1 were included.

Group 2 Alleles useful as differentials only in certain areas of the world. *Sr* genes 7a,7b,9a,10,13,14,15,17,23 and several others as yet uncatalogued were included here.

Group 3 Combinations of known alleles. These had two or more *Sr* genes per line.

Group 4 Combinations of unknown alleles which were found to react differentially from one region of the world to another. They were complex genotypes and included such cultivars as Thatcher, Chris, Selkirk, Timgalen and Gamut.

Group 5 Lines of unknown genetic constitution which were highly resistant to all strains in many locations. The group included lines of *Triticum turgidum* L. as well as many lines of *T. aestivum* L. from the International Spring Wheat Rust Nursery.

Group 6 Lines commonly used as susceptible parents in crosses and comprised Line E W3498, W2691 a Little Club derivative, Marquis and Chinese Spring.

All 117 lines of this collection had been tested with the available Australian strains that closely resembled those from Africa. As well they were tested with Angolan rusts numbers 1,3,4, and 6 and Rhodesia number 1. From the tests it was confirmed that the only genes effective in differentiation were *Sr*5, *Sr*7b, *Sr*15 and *Sr*BB. Angola 2 was not compared with culture 691042 in these tests but again no separation between members of the pairs was possible despite the extent of the genetic variability in the host material.

(v) *Comparisons of other Characters in the African and Australian Rusts.*

(a) Shape and Size of Uredospores. The length of the uredospores of Angola 3,4 and 6 were compared with the Australian cultures 73879 and 74220. On the basis of measurements on 50 spores of each there were no significant differences between Angola 3(33.48 ± 1.75μ) and 73879 (34.56 ± 2.18μ) and between Angola 6(34.32 ± 2.99μ) and 74220 (34.08 ± 2.91μ) at the P = 0.01 level although there was a marginal difference between the first two at P = 0.05. Angola 4(30.08± 2.06μ) was distinctly rounder than any other culture but it had no Australian counterpart. In width of spore all cultures examined fell within the range 17.64± 1.84μ – 18.68± 1.25μ.

(b) Uredospore Colour. There was no difference between Angola 2,3 and 6 and their Australian counterparts. Angola 4 and Rhodesia 2 with the same pathogenicity both differed from the other African rusts in having yellowish rather than brown uredospores.

(c) Growth in Axenic Culture. Uredospores of Angola 3 and 6 along with their Australian counterparts were sprayed separately onto Williams's (1971) agar medium in Petri dishes. The material was observed under the microscope 24 hours later and the structures showing were identical in all four cultures. This comparison as with those for pathogenicity, spore morphology and colour was of no value in demonstrating differences between corresponding rusts from the two continents.

Discussion and Conclusions

(i) *Pathogenicity and other Characters of the Cultures*. It is apparent from the results obtained that there is considerable diversity among the strains of *P. graminis tritici* in that part of the African continent represented by Angola and Zimbabwe. It was not the purpose of the study to examine in detail the extent of this variability but to compare African rusts with those from Australia where there were known counterparts.

Four Angola cultures 1(194-1,2,3,5,6,7), 2(194-1,2,3,5,6), 3(343-1,2,3,5,6) and 6(222-1,2,3,5,6) each had counterparts in Australia which were respectively cultures 74654, 691042, 73879 and 74220. When the overseas cultures were examined in paired comparisons with the corresponding local strains no differences in the members of each pair could be detected, even though the host material was very diverse. The uredospores were of the same size within reasonable limits of variation and although one Angola culture was clearly different from the others in spore shape, no counterpart for it was found in Australia. Growth in axenic culture which is sometimes useful in distinguishing between strains revealed no differences between local and introduced material. Although four counterparts were examined we are postulating that strains 326-1,2,3,5,6 and 194-1,2,3,5,6 arrived initially and the others 343-1,2,3,5,6, 194-1,2,3,5,6,7 and 222-1,2,3,5,6 evolved from them here by mutation.

(ii) *Significance of certain genes for Avirulence in the Australian environment*. Luig has already pointed out (1977) that when found late in 1969 the two cultures 69822 and 691042 carried the formula 1,2,3,5,6 from their infection on the local supplementals. This was a new combination for Australia. Virulence on plants with *Sr*6 (1) gave the first important hint in the field of this new material. In the previous four seasons 1965, 1966, 1967 and 1968 only seven isolates with this ability had been found east of the Nullarbor Plain among 1684 examined during the period (Luig and Watson, 1970). In addition both these new strains had another rare character, virulence on plants with *Sr*8. In the five years prior to 1969 only 12 isolates from a total of 2603 from throughout Australia were virulent on plants with this gene and not one of these could attack the *Sr*6 *Sr*8 combination. Thus to find these two cultures each with such a rare genotype *p*6 *p*8 was unexpected enough, but all the more so when one of them in addition had avirulence on plants with *Sr*7b.

It has previously been pointed out that during the 15 years prior to 1970 new patterns of pathogenicity arose in the Australian rust population due to the progressive introgression of new alleles into it (Watson and Luig, 1966). About 1950 the fungal alleles *p*5, *p*8, *p*15 and *p*BB predominated locally in *P. graminis tritici*. With the arrival of 21-0 all this changed since this strain brought with it *P*5, *P*8, *P*15 and *P*BB. It is clear from our studies that of the eight alleles at these four loci, seven of them were found in the African collections. *P*8 was missing. This all points to Africa also as the source of standard race 21 in the 1948-54 period and we strongly suggest this as a real possibility.

(iii) *The origin of strain 343-1,2,3,5,6.* It may be argued that our failure to recover this strain from the African material suggests some alternative origin for it. We pointed out earlier however that only three collections were available and these may not have been adequate to sample the area. If spores were windblown from Africa it would be expected that they would be of the most common strains. We know from Dr Santiago that components of race 194 had been present in Central Africa and in 1970 Fonseca (1974) found races 194 and 222 in Mozambique. To the best of our knowledge avirulence on plants with *Sr*7b had not been identified in the area. However the ease with which its presence was established in our collections demonstrates that it was part of the population at the time of these introductions. During the interval between the movement to Australia (1968-69) and the isolation in our tests (1972-73) the population may have shifted from 326-1,2,3,5,6 to 343-1,2,3,5,6 by simple mutation at the *P*5 locus. The demonstration of contrasting pathogenicity on plants with *Sr*7b requires good control over environment especially temperature and without it the four rusts of this family can easily be misclassified as shown in Fig. 1.

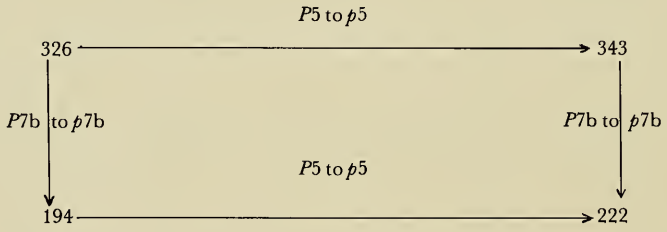

Fig. 1. Changes in Standard race number with single gene mutations at the locus indicated.

We believe that 326-1,2,3,5,6 entered Australia about 1968 multiplied on susceptible cultivates in southern states especially on Halberd (*Sr*6), mutated to virulence at the *P*5 locus and under selection pressure resulting from the cultivation of wheats such as Summit (*Sr*5) those mutants became apparent as 343-1,2,3,5,6 (73879).

(iv) *Other similarities between African and Australian rusts.* All the evidence we have presented and the evidence of Luig and Watson (1970) and Luig (unpublished) show a strong resemblance between the rust cultures we have compared. Unless gene flow has been involved, the similarity is much greater than would be expected in cultures originating in countries separated by the Indian Ocean. While this conclusion has been reached mainly from comparisons of pathogenicity, Burdon *et al.* (1982) have reached the same conclusion using isozymes as genetic markers. This new approach can also be used to trace evolution in rust populations. While these workers did not use material identical with ours their results completely confirm the close similarity between the strains of the two continents. No isozyme differences were found between the isolates of standard races 21, 194, 222, 326 and 343. Moreover two isolates from Angola *viz* 2 and

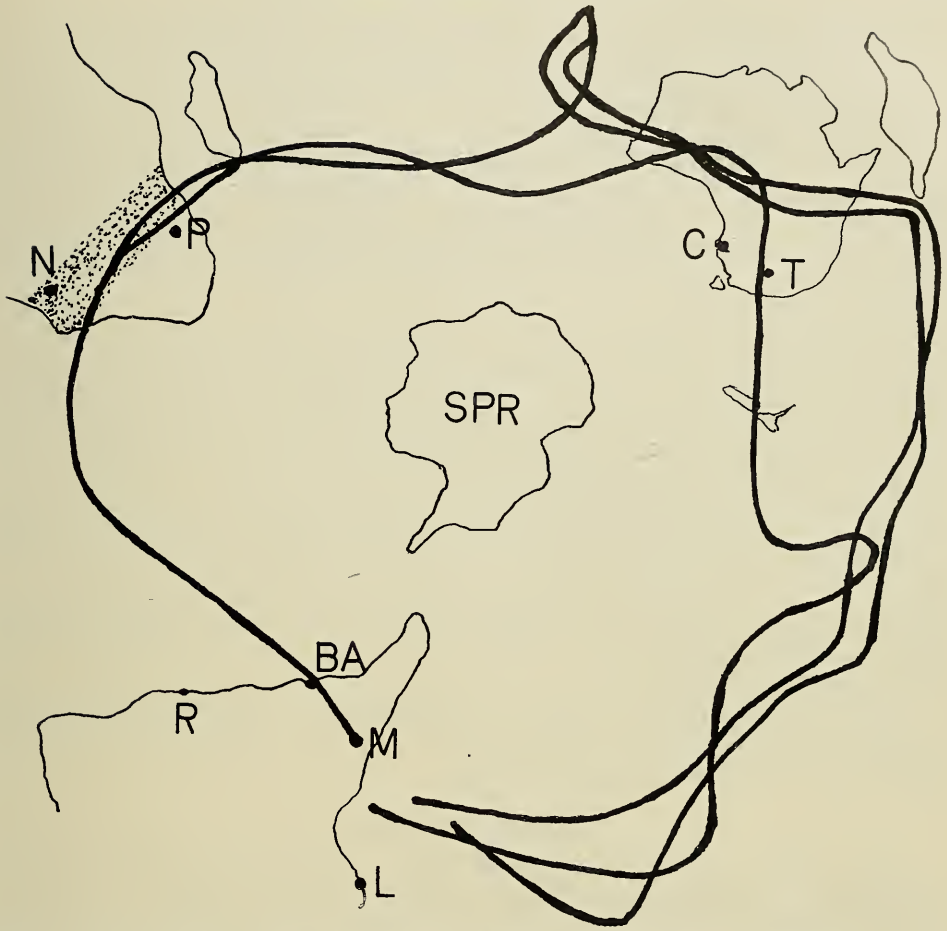

Fig. 2. Initial trajectories of 3 identical constant level balloons released almost simultaneously from Mendoza, Argentina on 20.9.71 (Partially redrawn from Morel and Bandeen, 1973).
C = Clinton, S. Aust., T = Tichborne, N.S.W., N = Nova Lisboa, Angola, P = Pretoria, S. Africa, R = Rio de Janeiro, Brazil, B.A. = Buenos Aires, M = Mendoza, Argentina, L = Lima, Peru, SPR = South Polar Region. Stippling indicates the probable source of spores.

4 were found to have the same phenotype as the following Australian rusts: 194-1,2,3,5,6 (S837 from Queensland), 326-1,2,3,5,6 (69822) and 343-1,2,3,5,6 (S1205 from Queensland). These workers have also proposed an African origin for strain 21-0 and this supports the conclusion we have also reached.

(v) *Weather conditions making spore transport possible.* The shortest distance between the wheat fields of Africa and Australia is approximately 12,000 km. To postulate natural movement of viable spores across this distance of water and the establishment of colonies from them in Australia we must assume 'a delicate synchrony of biological and physical processes' (Hirst and Hurst, 1967). It has been demonstrated that the rust strains from the two areas are indistinguishable, and it is known that physical processes are available to elevate spores of them from the crop to considerable heights. According to Ingold (1978) rust uredospores are set free around midday, and under relatively dry conditions vigorous thermals could carry the spores high into the air.

Schematic air paths shown by Ludlam (1967) suggest how they may be carried by rain clouds into the high troposphere, and possibly to the jet stream.

Once into the atmosphere there are a number of meteorological systems which could transport these spores to Australia. The first would be the anticyclones moving at a height of up to 3 km and covering the distance in about six days. While there will be a tendency for the spores to fall or to be washed out, circulation will have the effect of lengthening the period when they are airborne. The fall speeds of the spores would be of the order of 1 cm s^{-1} so that having reached an initial height of 5 km over the ocean, drift could carry them easterly for another 10,000 km. If they are in winds of 10 m s^{-1} and falling at 1 cm s^{-1} they would cross the Indian Ocean at the rate of about 1000 km each day (Pedgley, 1980).

As indicated above, some spores may reach the jet stream at a height of about 7–12 km and travel at much greater speed covering the distance in about two days. It has become apparent from the work of Lalley *et al.* (1966) and of Morel and Bandeen (1973) that jet streams in the southern hemisphere are much more continuous and rapid than originally estimated. Monitored balloons released in New Zealand and Argentina completed the global circuit in 10–12 days. Some of these trajectories are partially redrawn in Fig. 2, and show that the balloons may pass over the critical areas of both Africa and Australia. Presumably if spores reached the jet streams they could do the same, and eventually subside following air current originating in local thunderstorms. Once at ground level the spores would need to reach a congenial host on which to colonize. Apparently in 1968–69 the favourable climatic conditions which enabled Australia to produce a record wheat crop were also those allowing migrant rust spores to become established.

Intercontinental travel for spores of *P. graminis tritici* is hazardous and of rare occurrence. It is for this reason that we believe Australia has been involved in this migration only three times in the last 60 years.

ACKNOWLEDGEMENTS

The authors would like to thank Mr J. Colquhoun, Senior Research Meteorologist of the Department of Science, Sydney, and Dr I. Watson of the School of Earth Sciences at Macquarie University for help in interpreting the weather data. The work is based on a thesis submitted to the University of Sydney by the junior author for the degree of M.Agr. while holding a fellowship sponsored by the Food and Agriculture Organisation. We are grateful to Mr L. N. Balaam, Dean of the Faculty of Agriculture and Mrs Helen Keys for the typing of the manuscript.

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